



RESEARCH ARTICLE

Simple metrics to characterize inter-individual and temporal variation in habitat selection behaviour

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Abstract

1. Individual variation in habitat selection and movement behaviour is receiving growing attention, but primarily with respect to characterizing behaviours in different contexts as opposed to decomposing structure in behaviour within populations. This focus may be limiting advances in understanding the diversity of individual behaviour and its influence on population organization. We propose a framework for characterizing variation in space-use behaviour with the aim of advancing interpretation of its form and function.
2. Using outputs from integrated step-selection analyses of 20 years of telemetry data from African elephants *Loxodonta Africana*, we developed four metrics characterizing differentiation in resource selection behaviour within a population (specialization [magnitude of the response independent of direction], heterogeneity [inter-individual variation], consistency [temporal shift in response] and reversal [frequency of directional changes in the response]).
3. We contrasted insight from the developed metrics relative to the mean population response using an example focused on two covariates. We then expanded this contrast by evaluating if the metrics identify structurally important information on seasonal shifts in resource selection behaviours in addition to that provided by mean selection coefficients through principal component analyses (PCAs) and a random forest classification.
4. The simplified example highlighted that for some covariates focusing on the population average failed to capture complex individual variation in behaviours. The PCAs revealed that the developed metrics provided additional information in explaining the patterns in elephant selection beyond that offered by population average covariate values. For elephants, specialization and heterogeneity were informative, with specialization often being a better descriptor of differences in seasonal resource selection behaviour than population average responses. Summarizing these metrics spatially and temporally, we illustrate how these metrics can provide insights on overlooked aspects of animal behaviour.
5. Our work offers a new approach in how we conceptualize variation in space-use behaviour (i.e. habitat selection and movement) by providing ways of encapsulating variation that enables diagnoses of the drivers of individual-level variability in a population. The developed metrics explicitly distil how variation in a

behaviour is structured among individuals and over time which could facilitate comparative work across time, populations or strata within populations.

KEYWORDS

African elephant, GPS telemetry, individual variation, movement, resource selection, specialization, step-selection function

1 | INTRODUCTION

While characterizing the sources and magnitude of variation in behaviour has received growing attention, work to date has been largely exploratory and focusing on characterizing the behaviour observed in specific contexts, rather than the components of the behaviour that change between individuals or across contexts. Moreover, even with systems with strong individual variation, interpretation often collapses heterogeneity and focuses on the population-level inferences. A concern is that current approaches for assessing variation in behaviour may be stymying advances in understanding key aspects of individual behaviour, with particular relevance to dissecting interactions between conspecifics (but see Hertel et al., 2021). For instance, systematically focusing on population average response (and on its underlying assumption of normally distributed variation among individuals) fails to consider the possibility that individuals within a population might be purposefully differentiating behaviour to reduce competition (which would be reflected by a bi- or multi-modal distribution of behaviours; Bolnick et al., 2003). More critically, if such structure exists in a system, standard assumptions (e.g. that individual variation around a parameter follows a Gaussian distribution) behind popular modelling frameworks (mixed-effects models; Bolker et al., 2009) could be misleading in that population-level averages are not representative of any behaviour.

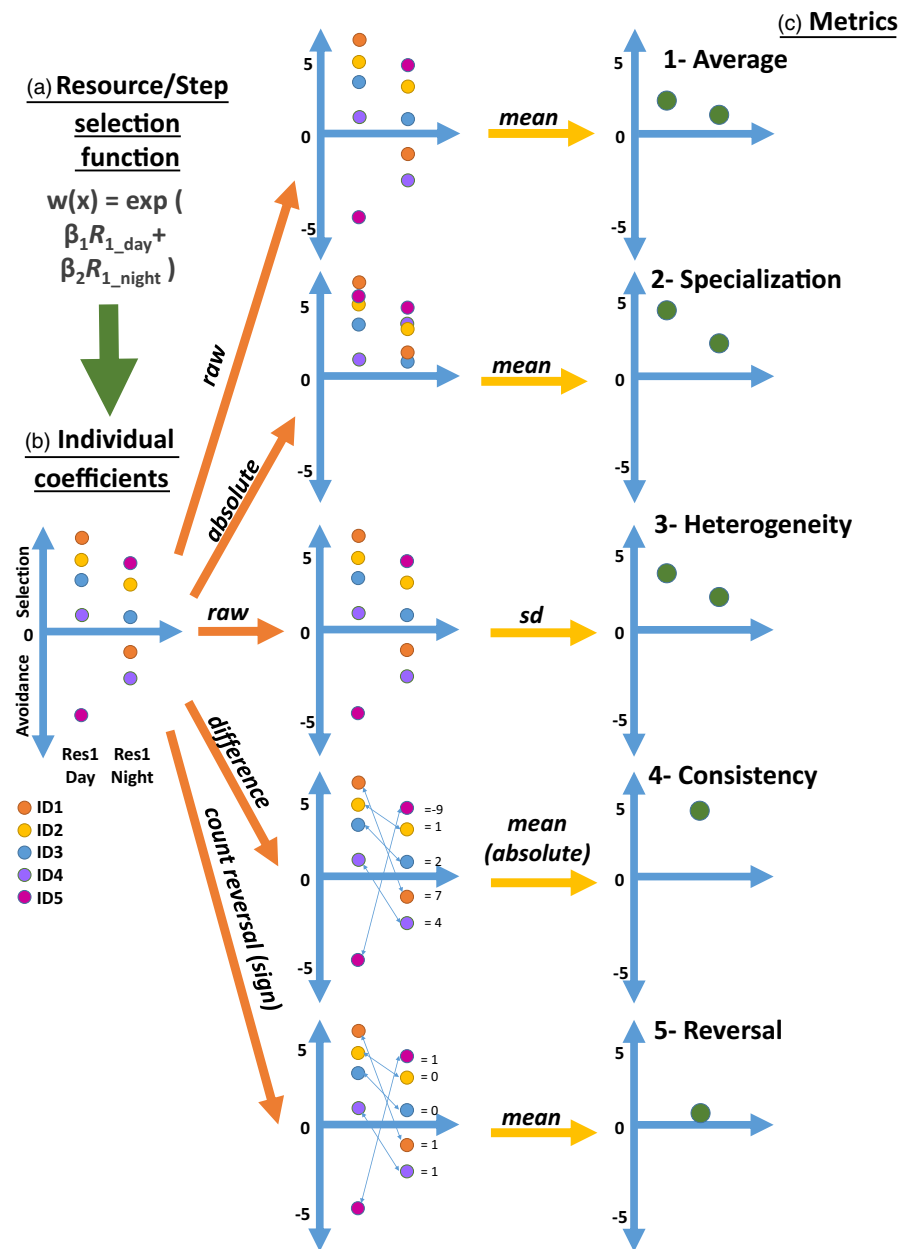
Ecologists considered variation in behaviour as a nuisance or a source of uncertainty, but studying variation in movement and its drivers has become one of the nexus between behaviour and ecology. In particular, structural differences between individuals in the behavioural process of resource (or habitat) selection and its associated movement has been shown to drive spatial partitioning and reflect differential strategies in populations (Bastille-Rousseau & Wittemyer, 2019). By temporally and spatially adjusting their use of resources, animals are able to balance multiple trade-offs (e.g. foraging opportunities with safety from predators; Laundré, 2010). While seasonal and diurnal characterization of resource selection is common (Courbin et al., 2009), characterization of finer temporal changes in resource selection, such as state-dependent or energy-dependent resource selection, offers deeper insight to behavioural drivers of population spatial structure (Grenier-Potvin et al., 2021; Hooten et al., 2018). Resource selection has also been shown to be influenced spatially by local context, a multiscale phenomenon referred to as functional responses in habitat selection (Moreau et al., 2012).

Lastly, variation in behaviour can be related to individual variation, whether because of differences in individual personality or plasticity (Hertel et al., 2020). Encapsulating individual resource selection behaviour or movement into a behavioural reaction norms framework has also improved the formal quantification of individual variation in resource selection, including the quantification of repeatability (Leclerc et al., 2016).

Ecology has a recurrent history of initially considering complexity as a nuisance more than the feature of interest. For example, while autocorrelation in movement behaviour has historically been considered as a statistical nuisance, Wittemyer et al. (2008) and Boyce et al. (2010) have shown that it possesses behaviourally relevant information. Notably, the structuring of variation in a behaviour of interest itself, like resource selection, might contain information that may better characterize nuances in a behaviour. For example, daily changes in movement and resource selection behaviour have been identified as core behaviours to balance foraging-risk trade-offs (Hebblewhite & Merrill, 2009; Ihwagi et al., 2018), where the changes in the behaviour itself are more informative to understanding the trade-off than the actual daily or nightly response. A similar logic could apply to seasonal changes in resource selection behaviour or movement, including changes in behaviour between periods of resource limitation and resource abundance (e.g. dry vs wet seasons). Given the potential of such fundamental processes driving structure in resource selection (and other) behaviours, we suggest that a more clearly defined approach to the systematic assessment of the temporal and inter-individual variation in behaviour is needed. The challenge is to find better ways of distilling this information.

Here, we propose a shift in how we study resource selection by proposing a framework focused on quantifying the aspects of the individual and temporal variation in resource selection behaviour within a population that can facilitate interpretation of its form and function and focus inter-population comparisons across time and space. We outline several new metrics of differentiation among individual behaviours and illustrate how these metrics provide unique insight to overlooked aspects of the behaviour (Figure 1). These simple metrics can be calculated from typical outputs of resource selection and movement analyses such as resource selection functions or step-selection functions (Fortin et al., 2005) providing individual-level coefficients. The presented metrics quantify (i) the magnitude of the response, not its direction (specialization), (ii) the extent of individual variation (heterogeneity) and (iii) temporal changes in behaviour (consistency and reversal).

FIGURE 1 Schematic illustrating the calculation of the developed metrics (specialization, heterogeneity, consistency and reversal) for a simple case evaluating resource selection for a single resource over two periods (here day and night). (a) A resource selection function or step-selection function is estimated using mixed-effects models (Muff et al., 2020) or individual-level modelling (Bastille-Rousseau & Wittemyer, 2019). (b) Individual-level coefficients are extracted for each individual and each time period. (c) For comparison purpose, a population average can be calculated for each time period by taking the mean of the raw values of the individual coefficients. Our first metric, specialization, can be calculated by taking the absolute value of individual coefficients and then averaging them. Heterogeneity is calculated by taking the standard deviation of the raw coefficients. Consistency and reversal are the metrics that evaluate differences in behaviour between the two temporal periods. Consistency is calculated by first taking the difference between an individual coefficient in the first and second period and then averaging the absolute of these differences among individuals. Reversal is calculated by first tallying whether an individual response is in an opposite direction (=1) or not (=0) between the two temporal periods and then averaging among individuals



To illustrate the utility of these new metrics, we evaluated space-use patterns using step-selection functions of African elephants *Loxodonta Africana* in northern Kenya. African elephants are recognized for displaying complex behaviours, including strong temporal and spatial variation in resource selection behaviour (Bastille-Rousseau & Wittemyer, 2019). Given the complexity of elephant resource selection in this system, it offers a salient case on which to evaluate the insights offered by the described metrics of variation in resource selection. To better highlight the aspects of behavioural differentiation the metrics captures, we first present a focused example assessing each metric on two covariates: vegetation productivity and elephant distance to village. We then expand our analysis to address two questions: (1) do the newly developed metrics provide additional information not captured by the population response across all covariates, and (2) is this additional information highlighting differences in complex

behaviours not captured by the population response. For this second question, we focused on highlighting differences among seasonal behaviours. For both questions, we used metrics derived from individual-level integrated step-selection analyses (ISSAs; Avgar et al., 2016) to jointly characterize resource selection and movement behaviour of elephants on a seasonal basis. We then used multivariate analyses to evaluate how these metrics provide different information from population average response. Given previous lines of evidence of purposeful differentiation among individual elephants in resource selection behaviour during the dry period (Bastille-Rousseau & Wittemyer, 2019) and of day-night switches in movement speed in response to risk (Ihwagi et al., 2018), we expected metrics of specialization and reversal to be particularly informative. We discuss how our proposed shift in how we evaluate and study resource selection or other behaviours can drive new insights to animal systems.

2 | MATERIALS AND METHODS

2.1 | Study area

The Laikipia/Samburu ecosystem in northern Kenya (approximately 0.4°S to 2°N, 36.2°E to 38.3°E) is inhabited by the country's second largest elephant population. Land use in the area include national (3% of study area) and forest reserves (4%), community conservancies (including management units within community conservancies such as delineated 'core' zones, 65%), private conservancies (<1%), private lands (5%), communal lands (11%) and government lands (11%). These land tenures differ in human predation risk for elephants (Ihwagi et al., 2015). The area has a variety of habitats, including cool moist highland forests and semi-arid savanna. The system generally experiences two wet periods and two dry periods annually, but with rainfall being highly stochastic (Bastille-Rousseau et al., 2020).

2.2 | Data collection

We analysed GPS data collected since 1998 from 156 elephants (425 elephants-years) in this area as part of a long-term research project. Elephant capture and handling protocols were approved by the Institutional Animal Care and Use Committee at Colorado State University (Amendment 1625, March 2022). GPS data collected from females represent a family unit of between nine and 15 individuals and males typically represent a single individual. On one occasion, more than one elephant was tracked simultaneously from the same family, which we controlled for by excluding one of the individuals for this analysis. Elephant families were considered as an individual unit, even if the collars were not always on the same individual. Erroneous locations were filtered by a speed filter of 9 km/hr. Individual elephant tracking datasets averaged 22,879 locations and 1005 days (range 179–142,654 locations, 18–4910 days) with a total sample of 3,591,945 locations. GPS locations were converted into trajectories where a step is the straight line between two consecutive locations. Only steps with a time interval between two locations of 1 hr were included in the analysis (i.e. locations taken at a higher resolution were resampled to 1 hr).

2.3 | Environmental variables

We compiled a series of spatial covariates to analyse elephant movement and resource selection. These covariates included a 30-m Landsat land cover classification reclassified into four landcover types: forest (7% of study area), wooded savanna (58%), open savanna (29%) and other types (6%). We also measured the Euclidean distance to roads and water sources. Roads were classified as primary (tarmac roads) and secondary (dirt roads). Water sources were characterized as permanent and seasonal sources. Roads and water sources were manually digitized from high-resolution land cover and verified where possible

by ground teams. We obtained elevation data at a 30m resolution from the Shuttle Radar Topography Mission (SRTM) and used them to generate a slope layer. Normalized difference vegetation index (NDVI) was extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation product (Justice et al., 1998). MODIS vegetation indices, which span the years 2000–2018, are provided at a 250m resolution every 16 days, yielding 23 composites per year. Temporal trends in NDVI data were also used to delineate wet, dry and transition periods using a clustering algorithm based on a normal mixture clustering (Fraley & Raftery, 2002). To quantify the change in human features in the area, human-associated features were digitized manually across the area using imagery available through Google Earth (see Bastille-Rousseau et al., 2020 for further details). We used this information to generate a layer of distance to villages and towns and layers of spatial density of permanent and non-permanent (i.e. seasonal) dwellings, which were extracted across a 500-m radius moving window.

2.4 | Movement and resource selection behaviour characterization

We evaluated resource selection and movement behaviour of elephants using an iSSA based on a conditional use-available design (Avgar et al., 2016; Fortin et al., 2005). We compared used locations to potential available steps sampled within the area the animal could have reached during that step. Available step lengths were sampled from a gamma distribution parametrized based on observed step lengths of the entire population. Turn angles for available steps were sampled from a uniform distribution ranging from $-\pi$ to π . For each used step, 25 random steps were generated. All spatial covariates, including biotic, abiotic and human features on the landscape, were extracted for all used and random locations. All continuous variables were centred and standardized (Schielzeth, 2010). The model also included an interaction between all covariates and a categorical variable (with six levels) combining day/night and seasons (wet, transition and dry). We fitted the same model to each individual-year separately (Bastille-Rousseau & Wittemyer, 2019; Fieberg et al., 2010) to derive individual by year coefficients using the R package IndRSA (link: <http://github.com/BastilleRousseau/IndRSA>).

2.5 | Characterizing the structure of variation in space-use behaviour

Investigations focusing on individual variation in resource selection behaviour frequently use individual-level coefficients as a response variable in univariate analyses (e.g. functional responses or behavioural reaction norms analyses; Moreau et al., 2012; Hertel et al., 2020) or in a multivariate fashion (Bastille-Rousseau & Wittemyer, 2019). Here, we looked at the patterns in variation in resource selection coefficients that capture how individuals use specific resources and how dynamic selection is over time. To accomplish this, we developed four metrics capturing structural aspects of variation in resource

selection behaviour: specialization, heterogeneity, consistency and reversal (Figure 1). While the population average is often representing a weighted mean of individual coefficients with their uncertainties (Murtaugh, 2007), in a simplistic case, this population-level response can be approximated by taking the mean of individual coefficients x_i , for a specific resource r at time period t and from n individuals:

$$\bar{x}_{rt} = \frac{\sum_{i=1}^n x_{irt}}{n}. \quad (1)$$

Following the same notation, we quantified 'specialization' as the magnitude of individual response to a resource, independent of its direction, calculated as:

$$\text{Spe}_{rt} = \frac{\sum_{i=1}^n \text{Abs}(x_{irt})}{n}. \quad (2)$$

Based on Equation 2, specialization should be strictly positive, with higher values indicating a higher degree of specialization. Relatedly, the 'heterogeneity' metric indicates the degree of individual variation (or degree of individual by year/season variation) in the response to a resource and calculated as:

$$\text{Var}_{rt} = \sqrt{\frac{\sum_{i=1}^n (x_{irt} - \bar{x}_{rt})^2}{n-1}}. \quad (3)$$

The heterogeneity metric is simply calculating the standard deviation of individual coefficients for a resource and will therefore also always be positive. The 'consistency' metric evaluates how similar the response for a resource is across temporal periods. For two temporal periods (e.g. day and night), the consistency is calculated as:

$$\text{Cons2}_r = \frac{\sum_{i=1}^n \text{Abs}(x_{irt_1} - x_{irt_2})}{n}, \quad (4)$$

where t_1 and t_2 represent the two different time periods. Consistency should also always be positive with values closer to zero indicating higher consistency between the two temporal periods. Similarly, for three temporal periods (e.g. among the wet, dry and transition seasons), consistency could be calculated as:

$$\text{Cons3}_r = \left(\frac{\sum_{i=1}^n \frac{\text{Abs}(x_{irt_1} - x_{irt_2}) + \text{Abs}(x_{irt_1} - x_{irt_3}) + \text{Abs}(x_{irt_2} - x_{irt_3})}{3}}{n} \right). \quad (5)$$

Lastly, 'reversal propensity' evaluates the propensity of individual switching from a positive selection for a resource during a given temporal period to a negative selection during another time period (or vice versa). For two temporal periods, reversal can be calculated as:

$$\text{Rev2}_r = \frac{\sum_{i=1}^n \begin{cases} 1 & \text{if } \text{sgn}(x_{irt_1}) \neq \text{sgn}(x_{irt_2}) \\ 0 & \text{if } \text{sgn}(x_{irt_1}) = \text{sgn}(x_{irt_2}) \end{cases}}{n}, \quad (6)$$

where sgn represents the sign of an individual coefficient for a specific resource and time period. Following Equation 6, reversal should be bounded between 0 and 1 with higher values indicating a higher rate of reversal. For three temporal periods, reversal is calculated as follows:

$$\text{Rev3}_r = \frac{\sum_{i=1}^n \begin{cases} 1 & \text{if } \text{sgn}(x_{irt_1}) \neq \text{sgn}(x_{irt_2}) \\ 0 & \text{if } \text{sgn}(x_{irt_1}) = \text{sgn}(x_{irt_2}) \\ 1 & \text{if } \text{sgn}(x_{irt_1}) \neq \text{sgn}(x_{irt_3}) \\ 0 & \text{if } \text{sgn}(x_{irt_1}) = \text{sgn}(x_{irt_3}) \\ 1 & \text{if } \text{sgn}(x_{irt_2}) \neq \text{sgn}(x_{irt_3}) \\ 0 & \text{if } \text{sgn}(x_{irt_2}) = \text{sgn}(x_{irt_3}) \end{cases}}{n * 3}. \quad (7)$$

2.6 | Propagation of uncertainties within each metric

Metrics described above do not account for the uncertainties associated with each individual coefficient (i.e. the standard error associated with a given coefficient). While it is possible to weigh coefficients based on their uncertainties and aggregate them to obtain population averages (Murtaugh, 2007), such weighting is impractical to implement for some of our metrics (such as reversal). Instead, we used a data augmentation procedure to account for uncertainties whereby we simulated 1000 replicates of individual coefficients based on a normal distribution centred on the coefficient values where we assigned the standard deviation as equal to the standard error associated with the coefficients. We calculated each metric for each replicate of the dataset. Metrics based on coefficients with generally small standard errors will have very similar values in each replicate and be more informative while metrics calculated from coefficients with larger standard error will have values that fluctuates more. This data augmentation approach is analogue to performing multiple iSSA using slightly different samples of data for each individual. We note that this propagation of uncertainty is especially helpful when comparing the metrics across covariates or temporal periods, but given the formulation of the metrics does not offer a straightforward way of assessing their significance. The dataset containing estimates of the different metrics for each replicate represents the basis of subsequent multivariate analyses. Code for implementation of each of these metrics is available in the IndRSA R package.

2.7 | Case study of metric application in the elephant system

To better highlight the interpretation of the different metrics and the type of insights they offer, we first provide a detailed overview of these metrics focusing on two of the 11 covariates estimated in the iSSA: vegetation productivity (as measured by NDVI) and distance to

village. Elephant responses to these covariates and, therefore, metrics of these response were expected to be divergent, with similar individual but different temporal responses to NDVI in contrast to stronger individual variation in response to village (Bastille-Rousseau et al., 2020). For each covariate, we summarized variation among each metric based on the 1000 replicates (as described above) and evaluated cross-correlation among each metric to assess the similarity (or dissimilarity) of information provided.

2.8 | Question 1: Are the metrics of variation in space-use behaviour providing additional information across all covariates?

We tested the hypothesis that the developed metrics will provide additional information on resource selection behaviour relative to the typical population average response. We applied principal component analyses (PCAs) to the metrics calculated for each covariate and each season of the iSSA to identify the metrics most informative for explaining variation in the resource selection behaviour. More specifically, for each covariate (e.g. landcover type, slope, NDVI...), we used a PCA to highlight if the new metrics provided information not contained by the average response (where the columns represent the different metrics and rows represent the 1000 iterations). This would be indicated by the main PCA axes not including average response as a significant contributor based on its eigenvector or by the population response generally being outperformed by other metrics in their contribution to the main PCA axes. Using each covariate-season, we extracted how frequently each metric (average response, specialization, heterogeneity, daily consistency and daily reversal) contributed significantly (contribution >5%) to the first three PCA axes, how frequently each metric was the biggest contributor to the first three PCA axes and how frequently each metric was within the top three contributors to the first three PCA axes. We also reported the average per cent of variation explained by each of the PCA axis. We implemented a standard assessment across three PCA axes to maintain consistency in outputs across covariate analyses.

2.9 | Question 2: Are the metrics of variation in space-use behaviour better at highlighting differences in seasonal behaviour?

We evaluated if metrics such as specialization, heterogeneity, consistency and reversal may be more informative than population averages in understanding shifts in elephant behaviour by applying a random forest classification algorithm to identify variables most important to explaining differences in elephant behaviour among seasons. We performed this analysis on three subsets of variables to facilitate identification of the key seasonal shifts structuring selection behaviour. These included the 'environmental' subset (landcover, slope, distance to water and NDVI), the 'anthropogenic

activities' subset (distance to road, density of bomas and distance to village) and the movement subsets (step length and cosine of turning angle). Random forest classification was done using 1000 trees and variable importance was measured using the Gini index (Han et al., 2016). A variable with a higher importance indicates a variable that is better (more important) at explaining differences in elephant behaviour among seasons. If the developed metrics provide useful information, we expect these metrics to be predominant in the variables with the highest importance. This part of the analysis was done using the RANDOMFOREST R package (Liaw & Wiener, 2002).

3 | RESULTS

After excluding individuals with insufficient amount of data (less than 100 observed steps in a given season), 334 elephant-years from 96 individuals were included in the analyses for a total of 1,984,614 observed movement steps. The number of individuals monitored on a seasonal basis were 333 elephant-years during the dry season, 334 elephant-years during the transition season and 334 elephant-years during the wet season.

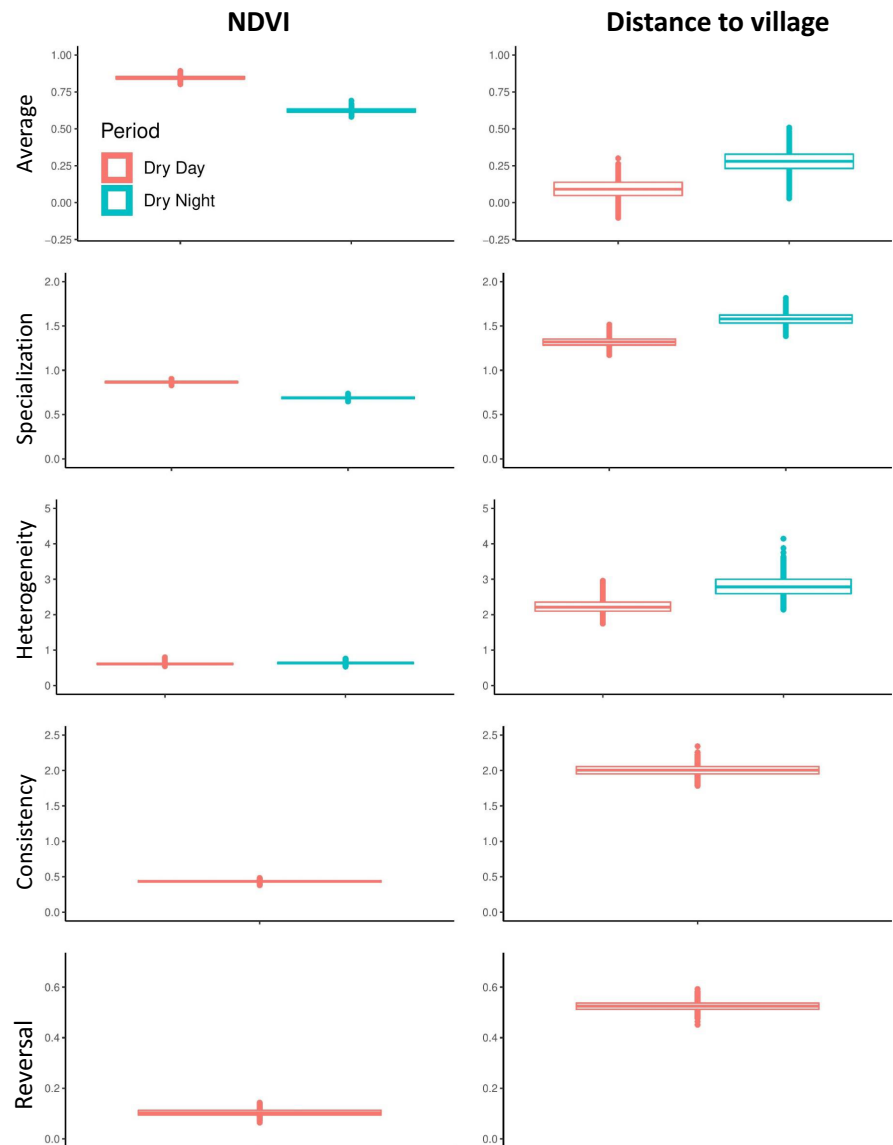
3.1 | Overview of elephant resource selection and movement behaviour

Average coefficient values from iSSA demonstrated that elephants displayed daily or seasonal variation in fine-scale resource selection for most resources (Figure S1). This included a generally weak response to land cover types (forest, wooded or other), strong selection for NDVI across seasons and time of day (with relatively tight confidence intervals around coefficient values, Figure 2) and consistent attraction to water (both seasonal and permanent) particularly at night. Elephants displayed variable selection for roads and avoided areas with higher density of seasonal or permanent bomas. However, confidence intervals were broad around coefficient values and elephants displayed strong diurnal shift in their response to (distance to) villages during the dry and transition season (Figure 2). Elephant generally moved longer distance during the day than at night, especially during the wet season. Patterns in turning angle remained relatively constant across time (Figure S1). Full results of resource selection behaviour as summarized by each metric are presented in Supporting Information, Appendix S1.

3.2 | Case study of metric application

Comparing the metric values for NDVI and distance to village highlighted the potential role of each of the metrics in understanding elephant behaviour (Figure 2). For NDVI, specialization largely mirrored average response for each time period and heterogeneity was relatively small (Figure 2), demonstrating the selection for

FIGURE 2 Boxplots of the metrics of variation of 96 African elephants inhabiting northern Kenya for two covariates estimated using an integrated step-selection analyses. Plots represent response of elephants to each covariate and the six metrics for the dry season during day and night (colour coded). Since the consistency and reversal metrics compare diurnal behaviour, only one boxplot is presented. Similar figures including the transition and wet periods are presented in Figures S6 and S7, Appendix S1. Boxplots are based on 1000 permutations where tighter plots indicate lower uncertainty in the results



vegetation was captured by the population-level average response. Lastly, consistency and reversal values were small, indicating that the selection for NDVI is relatively constant between day and night. For each of those metrics, the data augmentation approach showed limited uncertainty as shown by relatively tight whisker plots.

In contrast, the population average, which suggested no to weak response for distance to village, contrasted sharply with metrics of differentiation. Specialization was actually stronger for distance to village than NDVI (Figure 2) and markedly different from the population average (as indicated by non-overlapping uncertainties between the average and specialization). This indicates elephants showed opposite responses to villages. Relatedly, the heterogeneity value was higher than that of NDVI. Consistency and reversal were also higher for distance to village indicating stronger diurnal responses in elephant behaviour for this covariate (Figure 2), with over half of the individuals having an opposite response to village between day and night as indicated by reversal values >0.5 (Figure 2). These patterns were also evident from the cross-correlations analyses (Figure 3).

For NDVI, there was a strong correlation between average population response and specialization (indicating most individuals displayed the same response to vegetation), especially during the dry season while this correlation was weaker for distance to village (Figure 3). For both covariates, specialization tended to be correlated with heterogeneity (Figure 3), indicating that the individual variation observed was related to some individuals avoiding and others selecting for the resource.

3.3 | Question 1: Are the developed metrics providing additional information?

The application of a PCA to each covariate-season demonstrated that the first three axes captured around 73% of the variation in the observations (Table 1), but the population mean response was never the top contributor to PCA1 and PCA2 and rarely the top contributor to PCA3. Further, it was not identified as a significant

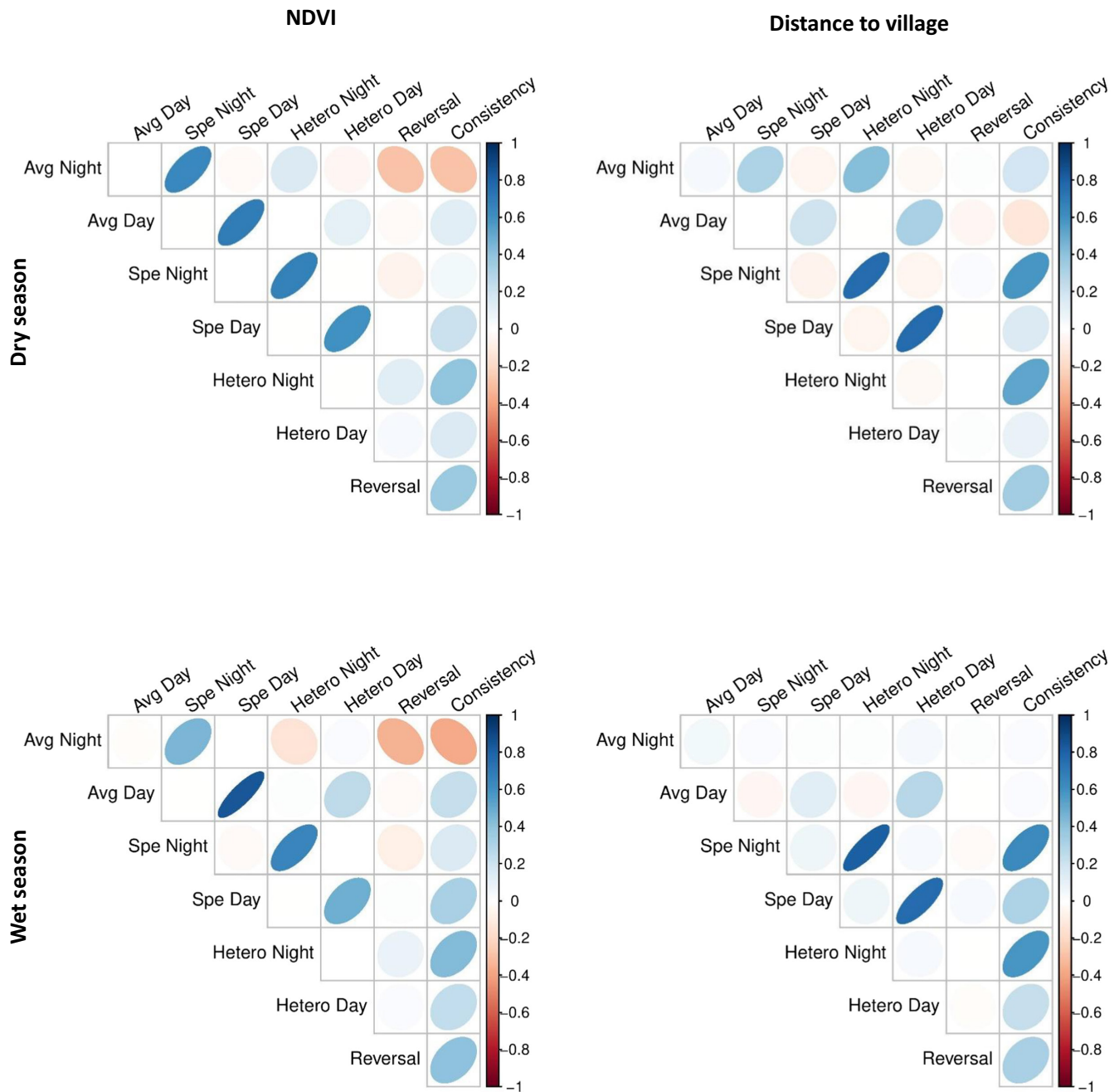


FIGURE 3 Cross-correlation plots showing correlation between metrics of variation (average [avg], specialization [spe], heterogeneity [hetero], reversal and consistency) of 96 African elephants inhabiting northern Kenya for two covariates estimated using an integrated step-selection analyses. Plots represent correlation for the dry season and two covariates (NDVI and distance to village). The magnitude of the correlation coefficient and its direction are colour coded and represented via an ellipse where a narrower ellipse represent a higher coefficient and the orientation of the ellipse the direction of the correlation. Similar figures including the transition and wet periods are presented in Figures S6 and S7, Appendix S1

contributor of the first three PCA axes in over half of covariates (59%), indicating that our metrics capturing different types of structure in the data tended to explain more of the variability in the iSSA results. The variables most likely to be a significant contributor of PCA1 were daily consistency, specialization at night and heterogeneity at night, while specialization during the day and heterogeneity during the day were most often considered a significant contributor to PCA2. Specialization during the night and

daily consistency were most often the top contributors to PCA1 while specialization during the day and heterogeneity during the day were most often the top contributors of PCA2 (Table 1). Interestingly, reversal was only an important contributor of PCA3 as indicated by each summary statistic (Table 1). This indicates quantification of differences in selection coefficients between individuals provided more explanation of selection behaviour than simply average values.

TABLE 1 Summary statistics of the contribution of each metric to three axes of a principal component analysis (PCA). PCAs were performed for each covariate of the integrated step-selection analysis to evaluate the interrelation among metrics. Summary statistics included how frequently a metric was significantly included (contribution >5%) in a given axis, how frequently the metric was the metric with the biggest (top) contribution to an axis and how frequently was the metric within the top three metrics. Average percentage of variation (and range) of each axis across covariates are also given

Variable	Inclu PCA1	Inclu PCA2	Inclu PCA3	Top1 PCA1	Top1 PCA2	Top1 PCA3	Top3 PCA1	Top3 PCA2	Top3 PCA3
Pop. mean night	0.405	0.238	0.524	0.000	0.000	0.071	0.024	0.214	0.524
Pop. mean day	0.310	0.571	0.333	0.000	0.000	0.000	0.238	0.452	0.310
Specializ. night	0.810	0.595	0.214	0.381	0.214	0.000	0.714	0.452	0.167
Specializ. day	0.548	0.857	0.095	0.190	0.405	0.000	0.310	0.690	0.024
Hetero. night	0.762	0.571	0.357	0.167	0.095	0.048	0.690	0.381	0.190
Hetero. day	0.476	0.762	0.071	0.048	0.286	0.000	0.238	0.714	0.048
Rev. day-night	0.000	0.024	1.000	0.000	0.000	0.833	0.000	0.000	1.000
Cons. day-night	0.929	0.071	0.786	0.214	0.000	0.048	0.786	0.095	0.738
PCA1% variation 0.327 (0.264, 0.473)									
PCA2% variation 0.249 (0.210, 0.302)									
PCA3% variation 0.151 (0.127, 0.215)									

3.4 | Question 2: Are the new metrics better at highlighting differences in seasonal behaviour?

Overall, across subsets of covariates, average response and specialization were most frequently the top variables with the highest importance scores, followed by heterogeneity and consistency in explaining seasonal differences in resource selection (Figure 4). Metrics of selection for the environmental covariates included NDVI and distance to permanent water (Figure 4), suggesting these were the two environmental factors driving differentiation in selection across seasonal fluxes. For the anthropogenic subset of covariates, average distance to primary road at night and specialization towards distance to village during the day were the two most important variables (Figure 4). Daily consistency in distance to road, specialization and heterogeneity in distance to primary road during the day were also among the top five most important metrics (Figure 4).

4 | DISCUSSION

Data acquisition and analytical innovations driven by improvements in technology are allowing remote observations of animal behaviour (such as GPS telemetry and camera traps) that have opened new avenues to addressing fundamental ecological questions (Wittemyer et al., 2019). This innovation and enhanced movement data collection is allowing more thorough understanding of differentiation between individuals in their spatial behaviour (Bastille-Rousseau & Wittemyer, 2019). Our goals were to develop new metrics to better characterize the structure of variation among the behaviour of individuals in a population. We focused our analysis on variation in resource selection and movement behaviour by wild African elephants. Our metrics characterized the type of variation found in resource selection coefficient values across covariates and highlighted specific

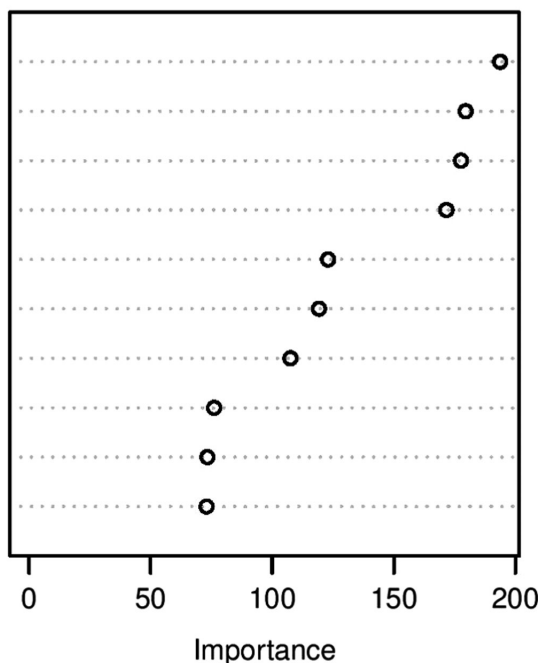
attributes of that variation in selection coefficients. Specifically, we quantified specialization (magnitude of the response independent of the direction), heterogeneity (individual variation in response), temporal consistency (temporal difference in response) and temporal reversal (frequency of change in the direction of the response). Our analyses revealed that these new metrics provided additional information in explaining the patterns found beyond that offered by the population average coefficient value, showing that this new information can more explicitly characterize complex behaviours that are often absorbed into variance estimates. In our study system of African elephants inhabiting northern Kenya, specialization and heterogeneity were particularly informative, with specialization often being a better descriptor of differences in seasonal resources selection behaviour than population average responses to covariates, potentially indicating that elephants diversify their niche space by displaying opposing tactics as exemplified with elephant response to village (Figure 2). Contrary to our prediction, reversal provided limited information in this study. While previous work in this system has described strong variation in elephant behaviour (Bastille-Rousseau & Wittemyer, 2019), the new metrics provide better ways of distilling and understanding how this variation is structured among individuals and over time. Overall, our work offers a fundamental shift in how we conceptualize and study variation in resource selection behaviour that has direct implications for myriad animal systems and behaviours.

4.1 | Structure of variation in elephant space-use

Elephant fine-scale resource selection evaluated via iSSAs provided results that were overall in agreement with previous studies in the same system (Bastille-Rousseau et al., 2020; Bastille-Rousseau & Wittemyer, 2019). Variables most important in shaping elephant

Environmental

- Speci NDVI Night
- Avg NDVI Night
- Speci NDVI day
- Avg NDVI Day
- Avg dist perm water day
- Speci dist perm water day
- Speci slope night
- Avg dist seas water day
- Cons NDVI
- Avg dist seas water night



Anthropogenic

- Avg dist prim road night
- Speci dist vill day
- Cons dist prim road
- Speci dist prim road day
- Hetero dist prim road day
- Cons dist vill
- Avg dist sec road day
- Hetero dist vill day
- Avg dist sec road night
- Speci dist prim road night

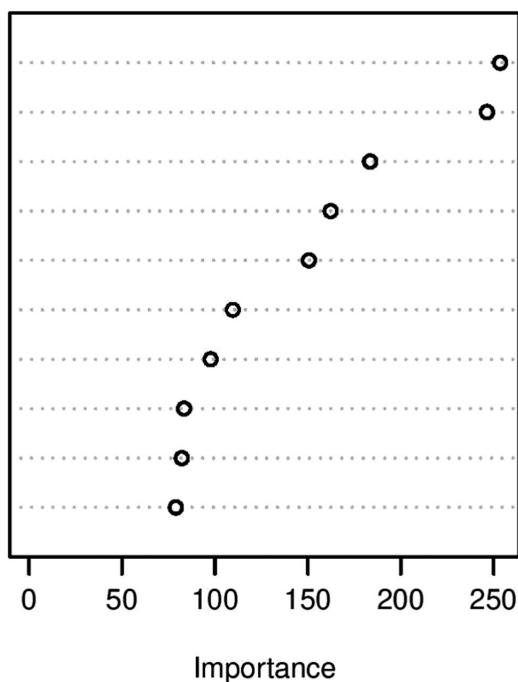


FIGURE 4 Importance of variables (based on the Gini index estimated using a random forest algorithm) in explaining differences among seasons. For each subset of covariates (environmental and anthropogenic), only the top 10 metrics are presented. Movement-related covariates are presented in Supporting Information, Appendix S1. Metrics included in the random forest analysis included average (avg), specialization (speci), heterogeneity (hetero), reversal and consistency (cons)

resource selection were mostly related to access to resources such as vegetation productivity (as assessed with NDVI) and water or related to avoidance of humans. In our system, elephant response to NDVI was uniform among individuals and over time relative to distance to village, which showed greater variation in individual responses. We leveraged this contrast in structure to highlight the applicability of our metrics. The analysis of distance to village offered

a clear example of where focusing inferences on the population average masked more complex patterns as shown by the strong specialization and heterogeneity observed for this resource. In contrast, specialization and population average were strongly correlated for NDVI, indicating little divergence from the population average in responses and less information from our metrics. Results of the PCA (Table 1) were further supportive of our first hypothesis that

the developed metrics provided different information. This was best indicated by the rare inclusion of the population average response (at night or day) in the top three contributors of PCA1 and PCA2 (Table 1) and by population average rarely being a significant contributor of PCA1. On the other hand, metrics of specialization, heterogeneity and temporal consistency were generally significant contributors of PCA1 or PCA2 and were most often the top contributor or within the top three contributors of these axes. Interestingly, for most covariates, PCA1 tended to include metrics associated with night behaviour (or daily consistency) while PCA2 tended to include metrics associated with day behaviour. This suggests distinct behaviours in elephant diurnal responses to multiple resources which covary diurnally. While behavioural variation in resource selection is often thought to be shaped by a subset of resources, for example resources used for foraging or safety (Bonnot et al., 2015; Hertel et al., 2021), the diurnal structuring in elephant behaviour reported here seems to supersede the different motivations elephants might have for different resources.

Results of the random forest classification moderately supported our hypothesis that the new metrics will be better than population average response in differentiating elephant behaviour among seasons for each subset of variables (environmental, anthropogenic and movement, Figure 3). Overall, population average and specialization were similar in explaining differences in elephant behaviour among seasons in regard to selection for environmental and anthropogenic variables and often for the same variables. For example, the top four environmental variables in importance were population average and specialization regarding NDVI during the night and day. As shown in our simplified example, the main reason for this is that response for NDVI was strong and fairly uniform across individuals and therefore population average and specialization contained similar information. This was however not the case for all resources, especially for anthropogenic variables. Specialization regarding distance to village was the second ranked anthropogenic variable in importance in the anthropogenic subset, but the average population response to this variable was not included in the top 10. As discussed above, this indicates that while elephants react strongly to villages, they adopted opposite tactics in their seasonal selection for villages. Even if the movement subset (Figure S8, Appendix S1) only contained metrics related to step length and turning angles, this subset had consistency in step length as the most important variable. Day–night shift in movement speed and tortuosity has been identified and suggested as a potential proxy of elephant response to risk (Ihwagi et al., 2019), with elephant increasing movement at night in risky landscape (Ihwagi et al., 2018). Our results indicate that this temporal shift is varying by season.

4.2 | Applicability to different contexts and systems

While our analyses indicated that the newly developed metrics provide complimentary information to the population average, how to

leverage and use this additional information to study animal behaviour is not intuitive. Specialization and heterogeneity can be easily integrated to existing workflows to perform resource selection analyses and could become routine metrics to report in addition to (or in some case possibly even instead of) the population average. We recommend that researchers consider and explore the possibility that specialization might provide information omitted in the population average response, and clarity on the uniformity, or lack thereof, of responses can be determined by evaluating and comparing both metrics. A species displaying strong specialization and heterogeneity in the absence of significant, average population selection/avoidance might be indicative of a system with strong intraspecific competition where individuals can potentially use resources differently or in systems where personality (e.g. boldness) can strongly shape resource selection (Bolnick et al., 2003). If specialization appears more informative than the average response, this indicates that focusing on the population average is misleading since it is failing to capture a bimodal (or more complex) pattern in a population response. Temporal consistency and reversal metrics do not conceptually integrate as easily into the typical workflow of resource selection analyses. Rather, their use might be limited to research focusing on the temporal structuring of specific behaviours.

Accounting for individual variation has become more popular thanks to improvement in mixed-effect models including random slopes (Muff et al., 2020), but quantifying its magnitude and structure has been less common. A formal accounting of the heterogeneity in responses can be beneficial given it is a source of uncertainty around the population average. Similarly, how resource selection analyses are often mapped to illustrate areas with higher and lower probability of use, spatial representation of specialization or heterogeneity can be informative about where behavioural variability may be greatest. Maps representing specialization highlight areas where individuals respond strongly (but potentially differently) to specific resources. Maps representing heterogeneity are complimentary to population average maps by representing areas with greater differentiation between individual predictions. In our system (Figure 5), mapping these metrics highlighted the similarity between specialization and average selection in most areas, and that differences between the two were more marked during the dry than wet season. Heterogeneity in resource selection also seemed to be lower in proximity to permanent water, suggesting similar behaviour across individuals included in the analysis in that area. These patterns, highlighting where selective behaviour is most acute and most variable across individuals, show that limited resources (like water in an arid ecosystem) can elicit similar responses, while increased differentiation in selection for outlying areas from such resources was apparent.

Taken altogether, these spatial representations of the different metrics could be informative for conservation purposes by identifying areas of consistent (areas with high specialization, low heterogeneity, high consistency and low reversal) or differentiated use that could characterize locations of general benefit. Areas with strong symmetry in behaviour are likely of fundamental importance, while differentiated areas likely relate to behavioural strategies. While we

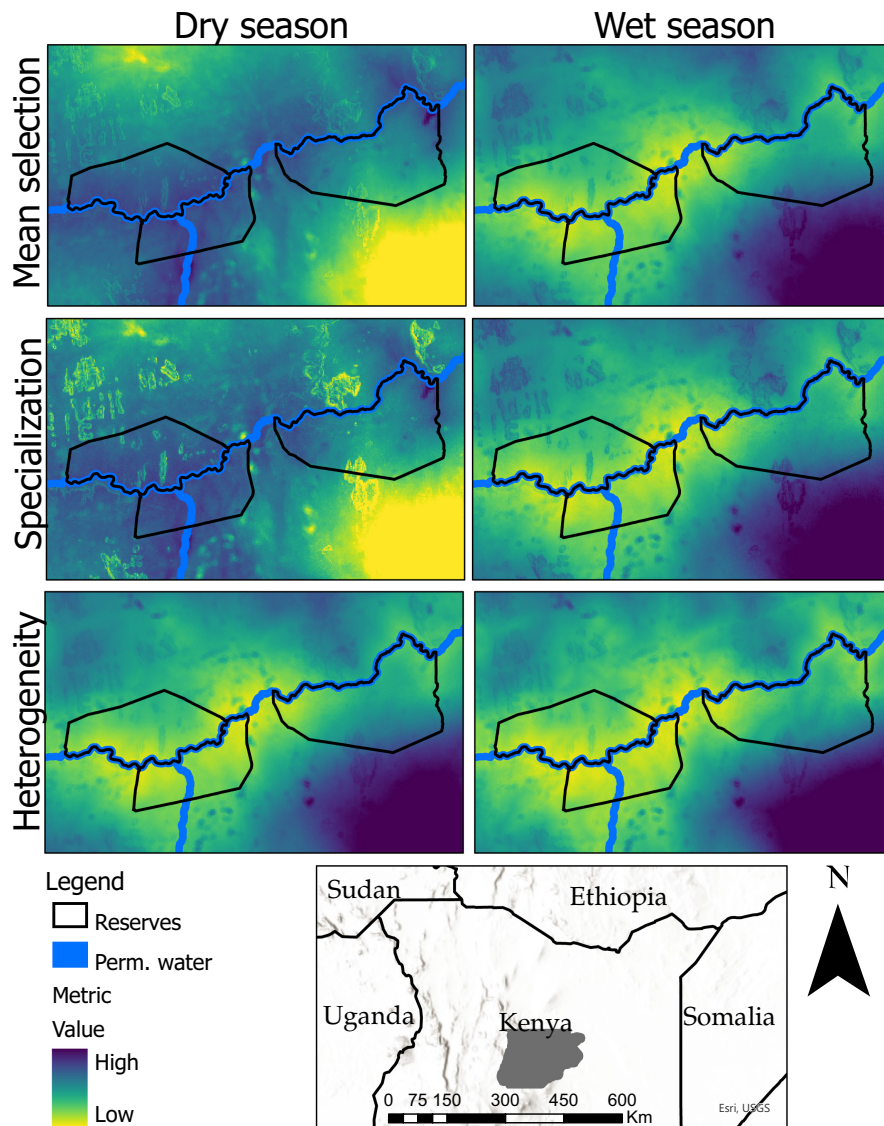


FIGURE 5 Spatial representation of population average, specialization and heterogeneity in resource selection of 96 elephants in northern Kenya. Metrics are presented for the dry and wet seasons during the day period. Population average represents a naïve estimate of elephant relative probability of occurrence (see Signer et al., 2017). Specialization represents the magnitude (independent of its direction) of elephant response to a location. Heterogeneity represents the variation in the use of an area among individuals. Location of the overall study area in northern Kenya is also represented

focused on diurnal structuring, consistency and reversal are easily applicable to other temporal periods such as seasons or even periods related to an animal life-history trait (reproduction or dispersal). Characterizing resource selection behaviour using different temporal subset of data has been the main way to deal with this temporal variation. Popular examples include examining resource selection over different periods because of expected change in predation risk (Hebblewhite & Merrill, 2009) or changes in resource value (Courbin et al., 2009). Our work represents an expansion from this line of work. Instead of contrasting two (or more) separate behaviours, we quantified the magnitude of the shift (or propensity of reversal) in a behaviour as a powerful means to summarize dynamics in animal behaviour.

The metrics developed here are relevant to a broader spectrum of behaviours than our application demonstrates. The metrics can be easily calculated for any behaviours or traits generally quantified over a continuous scale. Specialization and reversal are most meaningful when these values can range from negative to positive and with an opposite interpretation based

on the sign, but it would also be possible to standardize the values beforehand so that they are centred on zero. For example, our framework could be applied to metrics associated with social behaviour, such as association index or centrality measures of individual, and help better understand the social structure of a population (Aplin et al., 2013). Similarly, exploration of other characteristic behaviours, such as degree of vigilance or time spent foraging, with these metrics could provide a better understanding of the structure of variation in the behaviours within a population (i.e. foraging-risk trade-offs within a population). Overall, our work presents tools to better distil the information contained within individual-level variation in animal behaviour and progresses efforts to fundamentally shift how we study individual variation.

AUTHORS' CONTRIBUTIONS

G.B.-R. and G.W. designed the study; G.B.-R. performed the analyses and led the writing of the manuscript with contributions from G.W. Both authors gave approval for publication.

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CONFLICT OF INTEREST

No conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.vhhmgqnwb> (Bastille-Rousseau & Wittemyer, 2022). Elephant locations have been omitted from this dataset given their highly sensitive nature (there are high levels of poaching in the area). Functions developed in this manuscript have been integrated to the R package `INDRSA` <https://github.com/BastilleRousseau/INDRSA> or <https://doi.org/10.5281/zenodo.6452980> (Bastille-Rousseau, 2022).

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SUPPORTING INFORMATION

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